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PRESETTLEMENT REGENERATION PATTERNS IN A SOUTHWESTERN PONDEROSA PINE STAND[1]

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Abstract. Tree stems ≥106 yr old (i.e., established before significant European influence in this area) in a 7.3-ha old-growth ponderosa pine (*Pinus ponderosa*) forest in northern Arizona were aged and mapped. Age structure analysis showed that successful establishment of ponderosa pine was infrequent. The periods without successful establishment could be quite long, as suggested by four consecutive decades in which only two surviving trees were established.

The stems were strongly aggregated, as measured with nearest neighbor analysis, and groups were visually distinct in the field. Most of the stems occurred in groups of three or more, with group size ranging from 3 to 44 stems and area occupied by a group ranging from 0.02 to 0.29 ha. Ages of stems within groups were variable, the most homogeneous group having a range of 33 yr and the least having a range of 268 yr.

The data are not consistent with the commonly held view that southwestern ponderosa pine occurs in even-aged groups and that each group became established following the demise of the group previously occupying the site. Instead, it seems more likely that seedlings became established when one or two trees within the group died, the additional fuel surrounding the dead trees causing an intensely burned spot in the otherwise low-intensity fires that were frequent in the area. The hot spot would create a potential seedbed for pine by eliminating, at least temporarily, the competing grasses on that small area. This decreased competition, in conjunction with adequate seed production and favorable moisture conditions in the spring and early summer, may well have been critical for ponderosa pine establishment. The relative infrequency of all these events occurring in the necessary sequence could explain the erratic age structure data from this area.

Key words: age structure; Arizona; fire; old-growth stands; ponderosa pine; Pinus ponderosa; *regeneration; spatial distribution.*

INTRODUCTION

Natural establishment of ponderosa pine (*Pinus ponderosa* Laws.) seedlings in the Southwest is rarely successful (Pearson 1923, Heidmann et al. 1982). This is apparently because the factors necessary for successful establishment are relatively rare themselves and seldom occur in the necessary sequence. Problems in natural regeneration include erratic seed production (Larson and Schubert 1970), annual seedling-killing drought conditions in May and June (Pearson 1950, Schubert 1974), competition for moisture by perennial bunchgrasses (Larson and Schubert 1969), and various site-related factors, such as frost heaving (Heidmann 1976).

Despite these problems, seedling establishment and development to maturity must have occurred frequently enough to allow perpetuation of ponderosa pine forests. Historical accounts indicate that the pine forests were widespread in the Southwest at the time of early exploration and settlement (Cooper 1960). These forests were typically characterized as open and park-like with an understory rich in grasses (Cooper 1960). Although it is difficult to attach quantitative values to such a description, the description implies that these forests were probably not as dense as today's forests; nonetheless, some reproduction had to occur for these stands to exist. Given that adequate seed production and favorable moisture conditions had to occur occasionally, how were appropriate site conditions generated, especially if an abundant understory of grasses existed? Cooper (1960, 1961) hypothesized that suitable seedbeds were created when a group of old, large pines died simultaneously and produced enough fuel to create hot spots in the otherwise low-intensity fires that frequently swept through these forests. He used this reasoning to explain the mosaic of even-aged patches of ponderosa pine he observed in the White Mountains of eastern Arizona. The pine seedlings that became established on such areas would not experience the intense moisture competition that pine seedlings in grass-covered areas would, and consequently would have a greater chance for survival.

The purpose of the present study was to analyze the age structure and stem spatial distribution in an old-growth ponderosa pine stand in northern Arizona and make inferences from that analysis concerning the presettlement regeneration patterns that gave rise to the old-growth stands we see today. If Cooper's (1960, 1961) hypothesis were valid for this area, old pine trees of relatively similar ages could be expected to occur together in small patches.

STUDY AREA

The 7.3-ha study site was located in the Gus Pearson Natural Area (GPNA) about 15 km northwest of Flagstaff, Arizona. The area was chosen because it is relatively undisturbed, is typical of many sites in the ponderosa pine zone in northern Arizona, and has long-

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term records of tree mortality. The study area is at 2255 m elevation with a yearly average of 57.4 cm of precipitation (Avery et al. 1976), which typically falls as snow in the winter months and as rain in July and August (Schubert 1974). The average growing season is 94 d (Avery et al. 1976). The soils are montmorillonite clay loams of the Brolliar series which developed from late Tertiary lava flows (Avery et al. 1976).

The vegetation is dominated by ponderosa pine in the overstory and perennial bunchgrasses in the understory. The pattern of overstory vegetation is a mosaic with scattered clumps of old-growth trees separated by dense thickets of sapling-and pole-sized trees which originated primarily in 1919. These dense thickets are common in northern Arizona and apparently developed due to an unusual set of circumstances. A large seed crop was produced in 1918, followed by very favorable moisture conditions in 1919 and subsequent years (Pearson 1923). Survival of these seedlings was probably much greater than in presettlement days due to many years of heavy grazing, which reduced competition from grasses, and due to fire suppression efforts, which reduced the thinning effect of frequent fires. (See Madany and West [1983] for a discussion of the relative importance of these two factors.) This dense reproduction is not present, however, beneath the canopy of the old-growth trees, possibly because of the large litter buildup that occurs under these old trees in the absence of frequent fires.

METHODS

The tree population of interest was defined by age. Only trees ≥ 106 yr old (a center date of 1875 or earlier) were used because they had become established prior to any substantial influence by the early settlers, who arrived in the Flagstaff area in the late 1870's and 1880's (Cline 1976). Identification of this population required an indirect approach because it was not possible to age all the trees in the study area. First, all trees ≥ 37 cm dbh were chosen for initial study on the assumption that the majority of trees ≥ 106 yr old would have reached that size. Second, any trees <37 cm dbh that showed signs of the bark becoming yellow were also chosen for initial study. This second criterion was based on the common observation in the Southwest that ponderosa pine bark changes color from black to yellow as the tree ages (Pearson 1950).

All trees meeting one of the above criteria were cored at ≈ 30 cm above ground level. The cores were then sent to the University of Arizona Laboratory of Tree-Ring Research for aging using correlation techniques. Use of these techniques avoids the inaccuracies of direct ring counts due to false rings and locally absent rings (Stokes and Smiley 1968). From the age data, all trees ≥ 106 yr old were chosen for further analysis. Although some trees ≥ 106 yr old were undoubtedly missed by the sampling criteria, the age data supported the assumption that the vast majority of trees ≥ 106 yr old in the study area were included in the survey. Approximately 73% of the trees ≥ 37 cm dbh and 49% of the trees <37 cm dbh with yellow bark were ≥ 106 yr old; of 24 randomly chosen trees between 25 and 37 cm dbh without yellow bark, none was ≥ 106 yr old. The very large trees that were too big to core or that had rotten cores were also included in the study on the assumption that they met the age criteria.

Next, this population of trees originating prior to European settlement was mapped. Each group of three or more trees was mapped by starting with one tree and measuring the distance and direction from it to an adjacent member of the group. The process was repeated until all members of the group had been mapped. By actually constructing the map to scale as the measurements were made, an immediate check on the accuracy of the map was possible. The actual distance between the first tree mapped and the last tree mapped was compared to the distance determined from the map. If the difference was ≥ 1.2 m actual distance, the whole group was mapped again to reduce the error. The result was an accurate map of each group of trees. Each group was related to an existing grid system in the area by measuring the distance and direction from one member of the group to a marked corner in the grid system. By putting all these groups onto a composite map using the grid system as frame of reference, the actual position of each tree was accurately portrayed in relation to all other trees ≥ 106 yr old in the study area. The composite map was completed by adding the positions of trees occuring singly or in pairs by measuring distances and directions from these trees to grid system corners or to already-mapped trees.

The area occupied by each group of three or more trees was defined roughly by the area of influence of the group. This was easy to discern in most cases, because the dense thickets resulting from the prolific 1919 seed year had boundaries corresponding very closely to the canopy drip line of the larger, older trees. This drip line perimeter was mapped in the same way as were the trees in each group, i.e., by measuring distances and directions between points along the perimeter. The same degree of accuracy was required as with the individual tree mapping. The area of each group was determined from the map by tracing the perimeter of the mapped group with a compensating polarimeter. This was done three times for each group and the area was determined from the average of the three readings. In no case did the three readings differ by more than 3.5 units (equivalent on the ground to ≈ 0.001 ha).

The spatial distribution of stems in the entire study area, and of stems within each group of three or more individuals, was determined using the nearest neighbor method of Clark and Evans (1954). This method compares the actual average distance from trees to their nearest neighbor to the expected average distance if the individuals were distributed randomly; this ratio will be referred to hereafter simply as R. A random distri-

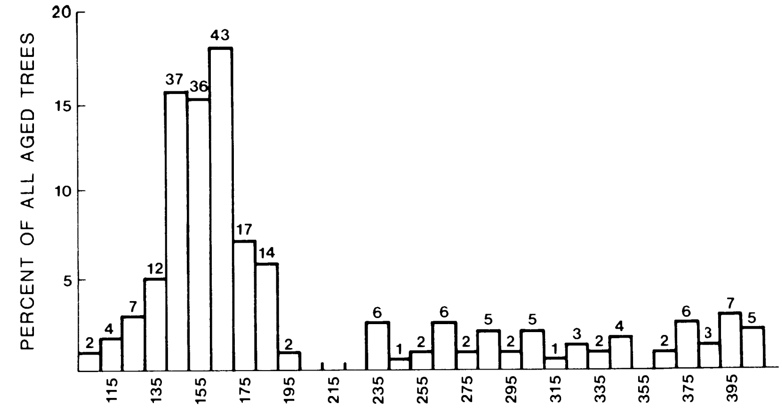

FIG. 1. Percent of total number (236) of aged trees ≥106 yr old occurring in 10-yr age-classes on entire study area. Number above each bar is the actual number of trees in that age-class.

bution would yield $R = 1$, whereas an aggregated distribution would yield $R < 1$ and a regular distribution would yield $R > 1$. This method has proven quite reliable in determining spatial distributions (e.g., see Goodall and West 1979). The major objection to use of this technique has been in situations where density had to be estimated from the distances themselves (Pielou 1969). This was not a problem in my study because actual density was known and did not have to be estimated.

RESULTS

The original population sampled included 373 trees, of which 268 trees were ≥106 yr old. Actual ages were available for 236 of these 268 trees; of the other 32 trees, 27 had rotten cores and 5 were too big (>101.6 cm diameter at 30 cm above the ground) for our increment borers to reach the pith. These 32 trees were included in the analysis because a count of the available rings or their large size left no doubt that they were at least 106 yr old.

Age structure by 10-yr age-classes is depicted in Fig. 1. Almost half the trees (49.2%) were between 141 and 170 yr old with a considerable drop on either side of this peak. A noticeable gap occurred between 191 and 230 yr; only two trees had ages in this range. Trees were quite evenly distributed between 230 and 410 yr. That 60% of the years had no trees established in them illustrates the sporadic nature of the age data.

TABLE 1. Characteristics of the 16 spatially distinct groups of three or more trees recognized in the field.

Group number	Number of trees	Group area (ha)	Density* (stems/ha)	Age ($\bar{x}$ ± SD)	Range of ages	R†
1‡	26 (26)§	0.15	178	156 ± 13	128–173	1.00
2	20 (11)	0.17	115	382 ± 24	335–404	0.88
3	44 (40)	0.29	153	189 ± 50	128–309	0.88
4	15 (15)	0.06	264	157 ± 13	127–180	0.64‖
5	3 (3)	0.02	148	246 ± 78	175–329	0.81
6	8 (8)	0.06	141	151 ± 14	121–163	0.99
7	14 (10)	0.06	216	354 ± 40	284–402	0.87
8	10 (10)	0.08	124	263 ± 21	231–289	1.34
9‡	30 (29)	0.11	285	160 ± 13	134–181	0.86
10	10 (5)	0.14	73	340 ± 113	138–406	1.20
11	20 (20)	0.14	145	169 ± 47	125–293	1.24
12	3 (2)	0.02	148	360 ± 26	342–378	0.71
13	19 (18)	0.17	114	156 ± 9	135–168	0.92
14	6 (5)	0.03	185	178 ± 53	145–271	1.17
15	4 (3)	0.04	110	310 ± 68	238–373	0.64
16	4 (2)	0.06	62	141 ± 45	109–173	1.08

* Density equals number of trees in a group divided by the area occupied by that group (calculations were done before area was rounded).

† Nearest neighbor ratio of Clark and Evans (1954); see Methods for explanation.

‡ These groups occurred adjacent to the boundaries of the study area. Consequently, number of trees and group area may be greater than indicated.

§ Number in parentheses refers to number of trees in each group for which age was available.

‖ Significantly ($P < .05$) different from 1.00 using test described by Clark and Evans (1954).

The distribution of stems ≥ 106 yr old over the entire area was strongly aggregated, as indicated by an R of 0.58. As mentioned in the Study Area Description, these groups were easily recognized in the field. Approximately 88% of the trees ≥ 106 yr old occurred in groups of three or more trees, with the groups occupying 22% of the 7.3-ha study area. A minimum group size of three was chosen because these were the smallest groups to exhibit characteristics of larger groups, namely the lack of 1919 regeneration under the canopy and a relatively well-developed understory of grasses and forbs. The remaining 78% of the area was densely stocked with sapling- and pole-sized stems and the 32 older trees not occurring in groups.

The 16 recognized groups differed in several respects (Table 1). Number of trees in a group ranged from 3 to 44 and area occupied varied between 0.02 and 0.29 ha, resulting in densities between 62 and 285 stems/ha. Average age within a group ranged from 141 to 382 yr and the range of ages within a group varied between 33 and 268 yr. The wide range of ages in each group was typically due to several different 10-yr age-classes being represented. For example, groups containing at least 10 aged trees had a minimum of 3, and as many as 12, 10-yr age-classes represented.

Spatial distribution within a group varied greatly (Table 1), the R values indicating aggregated, random, and regular patterns. However, only one of the values (for Group 4) was significantly different from 1 (using the test described by Clark and Evans [1954]). Whether this indicated a truly random distribution of stems within each group or was a reflection of the small number of stems within each group could not be determined. The maps of each group were also inspected to determine if trees of similar ages occurred together within the group, regardless of the distribution pattern. No evidence was found that indicated that these groups were composed of smaller groups with more homogeneous age structures.

The 32 trees not occurring in groups of three or more trees were found throughout the study area. These trees ranged in age from 106 to 406 yr, virtually the same range as was found for the trees occurring in groups (Table 1).

Discussion and Conclusions

The age structure data (Fig. 1) illustrate the great variation in successful establishment of ponderosa pine over time. Part of the variation is likely due to erratic seed production in presettlement years similar to the erratic seed production reported for this century (Larson and Schubert 1970).

Moisture could also have been limiting. To examine this hypothesis, the dendroclimatological record for the Flagstaff area (Drew 1972) was used to compare the best represented ages (141–170 yr) and the least represented ages (191–230 yr). Age at the 30 cm level was assumed to be between 1 and 10 yr. Thus, the "good years" were 1801–1840 and the "bad years" were 1741–1790. No clear correlations were found. The good period was characterized by three decades of below-normal precipitation, followed by one decade of above-normal precipitation. In contrast, the bad period had two decades of above-normal precipitation followed by three decades of below-normal precipitation. The lack of correlation may be because dendroclimatology is based on relating radial growth of mature trees to several precipitation periods during and immediately prior to the year of growth (Fritts et al. 1964). Precipitation during the critical period (May and June) for most young pine seedlings in the Southwest, however, may not correlate well with the precipitation periods that are well correlated with radial growth of mature trees.

Another possible explanation for the erratic age data is lack of good regeneration sites. That only 22% of the study area was occupied by old-growth trees supports the idea that only limited "safe sites" (sensu Harper 1977) were available for regeneration prior to European settlement. This was reinforced by the lack of evidence that earlier groups occupied much of the area between current groups (A. S. White, *personal observation*). Indeed, although numerous snags, stumps, and downed trees existed throughout the study area, the majority of such material seemed to occur around existing groups or around isolated trees (A. S. White, *personal observation*).

As described in many historical accounts (Cooper 1960), the area between groups in presettlement times was most likely occupied by grasses, which present a formidable barrier to successful pine seedling establishment. Cooper (1961) hypothesized that following the demise of existing groups, a relatively high-intensity surface fire created a suitable seedbed for pine seedlings to become established, given adequate seed production and moisture conditions. This resulted in the mosaic of even-aged groups of ponderosa pine in the White Mountains of Arizona.

In contrast to the pattern observed by Cooper in the White Mountains, my within-group age data indicate a wide range of ages within a group. A possible explanation is that rather than the whole group dying simultaneously, one or two trees within the group died and contributed enough additional fuel to a portion of the area to result in a high-intensity fire in that small area. The area thus created would typically be quite small and only capable of supporting one or two mature trees.

Several additional questions can be posed concerning mortality. In particular, are certain ages of trees not represented because seedlings established in that period of time were eliminated by some mortality agent before the seedlings reached maturity? Probably the best information available in this region on mortality agents in presettlement times concerns fire. Dieterich (1980) documented the fire history of Chimney Spring, only 6 km from the study area. His published fire frequency data indicate that during the previously noted good establishment years (1801–1840) the fire frequency was one fire every 2.2 yr, whereas during the bad establishment years (1741–1790) the frequency was one fire every 4.2 yr. Although at first glance this might seem to be an anomaly, perhaps the more frequent fires were less damaging to newly established seedlings because of less fuel buildup between fires. The difference in fuel buildup between fires at different frequencies could be great if old-growth groups were breaking down one or two trees at a time, rather than simultaneously, because the remaining live trees could be adding fuel to the small areas where seedlings were becoming established.

Establishment of ponderosa pine during presettlement times in the GPNA probably occurred as follows. First, adequate seed production was necessary; this eliminates years where virtually no seed was produced, but no data are available to suggest what the minimum number of seeds might have been in presettlement times. Second, the seeds had to germinate in an area where there was a reasonable chance of success. This required areas without significant grass competition. Most likely the grasses would have been eliminated only in small areas within existing clumps of mature trees where one or two individuals died and created a patch of heavy fuels that would burn intensely. Third, the years immediately following germination had to have sufficient precipitation in spring and early summer so that the young seedlings would not die from drought. Fourth, the seedlings had to avoid mortality during their early years. The greatest threat was probably from fire if fuel loads within the young patch of seedlings became too great, but certainly other factors, such as frost heaving (Heidmann 1976), also played a role. There is little evidence, direct or indirect, that suggests widespread mortality of ponderosa pine after the early, sensitive years. These four factors could have maintained the old-growth pattern observed in the GPNA today. Since the 32 trees that currently exist singly or in pairs were apparently once part of larger groups, the same four factors apply to them.

The data from this study may have some implications for wilderness and natural area management and timber management. For example, adequacy of natural regeneration in ponderosa pine natural areas may have to be judged over many decades. In timber management, a shelterwood cut may mimic natural conditions better than a clearcut, the success depending in part on whether or not fire is used as a site preparation tool.

Regardless of whether the proposed regeneration pattern of ponderosa pine in presettlement times proves to be true, the age structure of small, individual groups at the GPNA is contrary to the commonly held view that these groups are even aged (Schubert 1974). The range of ages within many of the examined groups is simply too great for even a very liberal interpretation of the term even aged. One possible reason why the data in this study do not concur with Cooper's (1960, 1961) findings in the White Mountains is that the two areas represent quite different sets of environmental conditions. For example, precipitation patterns are different. Summer rains tend to start earlier in the White Mountains than in the Flagstaff area (Schubert 1974). The influence of environmental conditions on regeneration patterns could help explain why ponderosa pine does not have the same types of age structures and stem distribution patterns throughout its range. The concept of the southwestern ponderosa pine forest as a mosaic of groups (Schubert 1974) is upheld by the study of stem spatial distribution, but the age data indicate that groups in at least one area are not even aged.

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